

A NEW GEOGRAPHIC FORM OF THE SPINNER DOLPHIN, *STENELLA* *LONGIROSTRIS*, DETECTED WITH AERIAL PHOTOGRAMMETRY

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ABSTRACT

Analyses of skeletal and external morphology of spinner dolphins killed in the yellowfin tuna purse-seine fishery in the eastern tropical Pacific led to the description of two subspecies of spinners from this region, the eastern spinner dolphin and the Central American spinner dolphin (Perrin 1990). However, when we examined lengths of spinner dolphins taken from vertical aerial photographs from the same area, we found three unique morphotypes. Two of these forms correspond, at least in average length and distribution, to the existing subspecies. The third form is intermediate in length between the two recognized subspecies and is found along the edge of the continental shelf north of Cabo Corrientes, Mexico. We provisionally call this form the "Tres Marias spinner dolphin." Our results demonstrate the value of a mix of fishery and fishery-independent data in studies of stock structure of impacted species.

Key words: spinner dolphin, *Stenella longirostris*, stocks, length, aerial photography, photogrammetry.

Our knowledge of the intraspecific structure of spinner dolphin populations in the eastern tropical Pacific (ETP) is based almost entirely on data taken from specimens killed in the yellowfin tuna purse-seine fishery (Perrin 1969, Lo and Smith 1986). Two subspecies of spinner dolphin are recognized from this region: the Central American spinner dolphin (previously known as the Costa Rican spinner dolphin), *Stenella longirostris centroamericana*, and the eastern spinner dolphin, *S. l. orientalis* (Perrin 1990). A third form, the "whitebelly spinner," is thought to be a result of hybridization or intergradation between the eastern and pantropical (*S. l. longirostris*) spinner dolphins (Perrin 1990, Perrin *et al.* 1991, Dizon *et al.* 1991, Dizon *et al.* 1994). The Central American

spinner is endemic to nearshore waters (within 92 km of the coast) from the Gulf of Tehuantepec to Panama. The eastern spinner is found in a roughly triangular region that has its western apex at around 10° north latitude and is bounded on the east by the coastlines of Mexico and Central America (Perrin *et al.* 1985).

From the data based on specimens, it appears that spinner dolphins vary geographically in external and skeletal morphology (Perrin *et al.* 1991, Douglas *et al.* 1992), in color pattern (Perrin 1972), in reproductive seasonality (Perrin *et al.* 1977, Barlow 1984), and in other aspects of reproduction and life history (Perrin and Henderson 1984). Although the high mortality suffered by this species in the ETP purse-seine fishery has provided an ample supply of specimens for study (Lo and Smith 1986; DeMaster *et al.* 1992; Wade 1993, 1995), it is reasonable to question whether findings based entirely on specimens from a fishery targeted on tunas are fully representative of the dolphin populations sampled, and whether conclusions drawn from these data can be generalized to adjacent environments (Barlow and Hohn 1984, Perrin and Reilly 1984). Certainly the geographic distribution of the samples reflects the regions in which spinner dolphins are found associated with commercial quantities of yellowfin tuna (Punsly 1983). Furthermore, the offshore pantropical spotted dolphin, *S. attenuata*, is the preferred species for tuna fishermen, because it "carries" more tuna than the spinner dolphin. Thus, a large proportion of the spinner dolphin specimens collected in the fishery are from schools in which they are mixed with spotted dolphins, often as the minority species. It is possible that spinner dolphin samples taken from mixed schools are not representative of the species as a whole in the region.

To determine whether our current understanding of spinner dolphin stock structure derived from fishery samples is a biased one, we examined length distributions from vertical aerial photographs of schools of spinner dolphins within the core eastern spinner geographic region (Perrin *et al.* 1991) and from two adjacent coastal habitats, the known habitat of the Central American spinner and a more northerly coastal region. We then compared our length data with lengths of specimens taken in the fishery. This analysis led to detection of a previously undescribed form of spinner dolphin from the ETP.

METHODS

The dolphin lengths presented in this report were measured from vertical aerial photographs of 29 schools of spinner dolphins photographed between 1988 and 1993 (Table 1). We used military reconnaissance cameras mounted below the hull of a Hughes 500D helicopter. The helicopter was carried aboard the NOAA Ship *David Starr Jordan*. This sampling was part of a larger program conducted by the National Marine Fisheries Service (NMFS) to monitor trends in abundance of the dolphin populations that suffered heavy mortality in the yellowfin tuna purse-seine fishery in the eastern Pacific (Wade and Gerrodette 1993).

We used modified U.S. Navy cameras (KA-45A) during the first five years

Table 1. Photo dates, positions, school size, and composition of schools photographed and used in this report. School size was determined from counts made on the aerial photographs.

School #	Date	Latitude-N	Longitude-W	School size	% Spinners ^a
1	15 Oct. 1993	23°54'	107°36'	944	100
2	15 Oct. 1993	23°44'	107°36'	832	100
3	15 Oct. 1993	23°13'	107°30'	529	98
4	3 Aug. 1992	21°18'	105°52'	1,715	100
5	27 Sep. 1993	23°00'	109°29'	515	24
6	3 Oct. 1993	22°18'	108°00'	156	51
7	27 Aug. 1993	20°30'	109°17'	171	100
8	29 Aug. 1993	19°55'	109°58'	83	100
9	4 Aug. 1989	17°35'	115°37'	153	100
10	8 Nov. 1988	17°07'	101°59'	204	90
11	8 Nov. 1988	17°14'	102°12'	287	100
12	1 Nov. 1990	16°51'	104°20'	48	100
13	8 Nov. 1988	16°59'	101°46'	128	100
14	31 Oct. 1990	16°14'	101°42'	87	92
15	31 Oct. 1990	16°22'	102°22'	34	100
16	4 Nov. 1989	12°45'	108°23'	315	100
17	10 Nov. 1990	11°28'	106°58'	79	100
18	25 Oct. 1992	15°11'	99°45'	20	100
19	10 Nov. 1988	14°31'	99°21'	206	95
20	10 Nov. 1988	14°27'	100°07'	341	77
21	6 Aug. 1992	15°40'	97°43'	175	96
22	6 Aug. 1992	15°32'	96°55'	267	100
23	10 Aug. 1992	11°33'	93°21'	250	100
24	10 Aug. 1992	11°28'	93°45'	2,170	88
25	10 Aug. 1992	11°21'	93°45'	2,064	93
26	25 Aug. 1992	14°00'	90°00'	2,089	100
27	25 Aug. 1992	12°58'	90°06'	300	100
28	25 Aug. 1992	12°59'	89°58'	6,011	100
29	25 Aug. 1992	13°08'	90°00'	4,921	100

^a Balance were pantropical spotted dolphins, *S. attenuata*.

of the study. In 1993 these systems were replaced with newer, but nearly identical, U.S. Army cameras (KA-76). Both cameras use the PAXAR 152-mm (f2.8) fixed-focal-length lenses and have forward image motion compensation systems. We photographed dolphin schools from altitudes of 200–300 m. We used Kodak Plus-X Aerechon II thin-base film throughout the study. More details on the cameras and photographic techniques are presented in Perryman and Lynn (1993, 1994).

Prior to making any measurements, we reviewed the photographs from all of the passes over a school and selected the pass which captured the largest number of dolphins swimming close to the surface. We attached a clear acetate sheet over the first photograph of the selected pass and assigned a number to each dolphin that could be measured. The acetate overlay was then moved

sequentially through all the images in that pass until a map of numbered dolphins for the school had been created.

We made measurements on the original black and white negatives using an STK stereo comparator. Because the dolphins moved between adjacent overlapping images, the measurements were made on single images rather than on stereo pairs. The acetate overlay for the school was placed over each frame, so that each measurement could be identified with the number assigned to that dolphin. We measured the length of each dolphin from the tip of the rostrum to the trailing edge of the tail flukes. We selected the trailing edge of the flukes, instead of the base of the fluke notch, because we could detect the former reliably in the images. Selection of this point of measure adds a positive bias of about 3.2% for large dolphins (> 150 cm) and 4.4% for small ones (Scott and Perryman 1991).

We attempted to measure only those dolphins that were at shallow depths and swimming parallel to the surface. However, we probably measured some dolphins that were slightly flexed or at a slight angle to the surface, and these lengths will be negatively biased. Because the area covered by adjacent photographs overlapped by 80%–90%, we measured many dolphins on more than one frame (*i.e.*, measurements were taken on two to four adjacent frames). We tried to minimize the potential bias described above by selecting the longest measurement for each of these dolphins. To be certain that our data were not biased by measurements from frames with scale errors (errors caused by the camera not being parallel to the sea surface or by anomalous altitude readings), we compared measurements from all of the frames within each pass. When comparing length samples from different regions, we assumed that measurement bias was consistent between samples.

To convert lengths measured on the photographs to lengths at the sea surface, we multiplied the measurements by a scale factor (altitude/focal length of the lens). Altitude was determined by a radar altimeter and recorded by a computer-based data acquisition system as each frame was exposed (about one frame/sec). We scanned the altitude data for each pass and replaced the occasional spurious reading with the mean of the two adjacent recorded altitudes. The relationship between altitude and the voltage output of our altimeter (Sperry AA300) was linear throughout its range. To correct for bias in the altimeter, we photographed known-sized objects and determined the relationship between scale based on altimetry and scale calculated from known distances (see Perryman and Lynn 1993).

In 1992 and 1993 we calibrated the altitude data by conducting a series of photographic passes over two 15-m sections of plastic pipe that were towed away from the ship with a small inflatable boat. Altitude calibrations were completed on 8 August, 23 September, and 26 October in 1992 and on 23 July, 15 August, 11 September, and 7 and 17 September in 1993. Based on the relationship between altitudes calculated from measurements of these known-sized targets on the aerial photographs and altitudes recorded from the altimeter, we developed correction factors for the recorded altitude readings (Gilpatrick 1996). The linear regression equations that describe the relation-

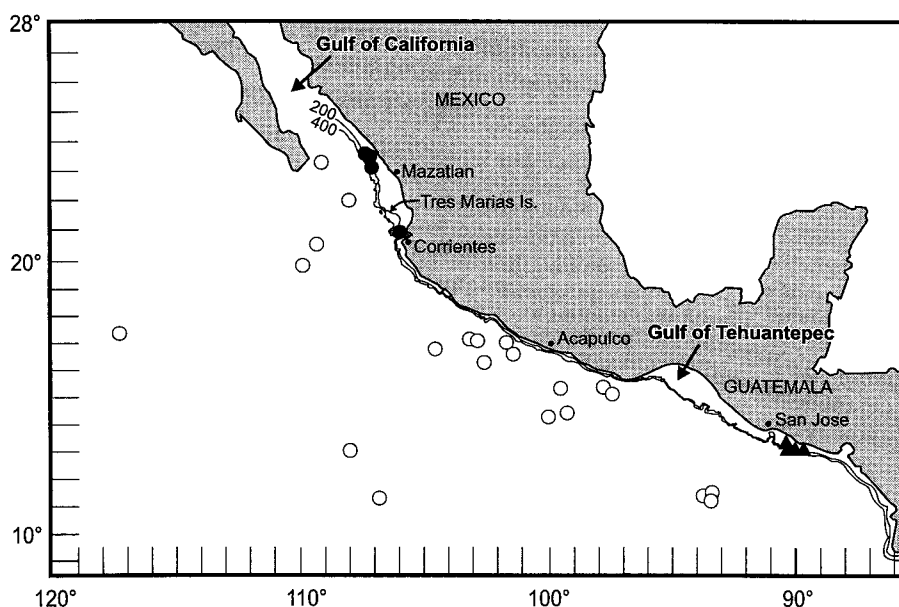


Figure 1. Distribution of photographed schools used in this report. Schools are identified by area: northern inshore (●), offshore (○), and southern inshore (▲). The 200- and 400-fathom contours are shown.

ship between altitude calculated from target measurements (A_m) and recorded altitude (A_r) are shown below.

1992 season

$$A_m = 0.987A_r - 7.982 \quad (n = 32; r^2 = 0.994) \quad (1)$$

1993 season

$$A_m = 0.994A_r - 15.757 \quad (n = 82; r^2 = 0.991) \quad (2)$$

Subdivision of photographic samples—The core habitat of the eastern spinner dolphin, as described above, is the most tropical and exhibits the least oceanographic variability of those found in the ETP (Wyrski 1964, Au and Perryman 1985, Reilly 1990). Along the coast, the Middle America Trench lies close to the coast of Mexico from Cabo Corrientes to the northern boundary of the Gulf of Tehuantepec (Fisher 1961, Chase 1968). North and south of these points, the coastline shifts to the east, creating large continental shelves. For our analysis of spinner dolphin lengths, we compared samples from these two shallow-water habitats with the sample taken from the offshore area (Fig. 1). Having divided our sample in this way, we tested the prevailing assumption that the spinner dolphins found along the shelf near the mouth of the Gulf of California (the northern inshore area) are members of the eastern spinner subspecies rather than more closely resembling the Central American form found along the shelf south of the Gulf of Tehuantepec (the southern inshore area) (Perrin *et al.* 1991, Dizon *et al.* 1994).

Length comparisons—photographic samples—We used an analysis of variance

(ANOVA) to test for differences between the means for the three regional length strata described above. To eliminate calves and small immature dolphins from the sample, we used lengths > 140 cm. The selection of this criterion for eliminating young dolphins from our test was somewhat arbitrary, but we have found that tests for differences between well-defined distributions are relatively insensitive to the precise value of this cut-off point (Perryman and Lynn 1993). We used a Tukey-Kramer test for pairwise comparisons, because its power remains high when sample sizes are unequal (Day and Quinn 1989).

Length comparisons—photographic samples and specimen data—We conducted a second single-factor ANOVA to compare lengths of dolphins from our three regions with lengths of dolphins killed in the purse-seine fishery. For this comparison we used only data collected from sexually mature female dolphins, because we can confidently identify them as such in both the fishery specimen data and the aerial photographic data. For the fishery sample, sexual maturity in females was determined by examining both ovaries for the presence of one or more *corpora albicantia* or a *corpus luteum* (Perrin *et al.* 1976). The sample of total body lengths for sexually mature specimens includes data published in Perrin *et al.* (1985) and data collected subsequently (SWFSC, unpublished data). We identified dolphins as adult females in the photographs based on the characteristic swimming formation of cow-calf pairs. We assumed that the larger dolphin swimming in close association with a calf was an adult female. Because this determination is based only on behavior, we qualify the term with quotation marks ("adult female") whenever we refer to a sample of lengths based on this assumption.

This method of identification introduces a slight positive bias into the photographic data when compared to the identification method used with the fishery specimen data. Females identified as adults in the aerial photographs have carried a calf to term and given birth, whereas female specimens identified as mature using histobiological evidence of ovulation may have completed only their first ovulation and may still have been growing. However, for eastern spinner dolphins, the difference in average length for lactating and sexually mature female specimens in the database for dolphins killed in the tuna fishery is small (0.2 cm), and this difference is not statistically significant ($t = 0.814$, $P = 0.42$) (SWFSC, unpublished data).

RESULTS

The null hypothesis that the means of the truncated length samples from our three geographic regions (Fig. 2) did not differ was rejected ($P < 0.001$). *Post hoc* tests (Tukey-Kramer) revealed that all three means differed significantly from one another (Table 2).

The second hypothesis of no differences in average length between sexually mature female eastern and Central American spinner dolphin specimens from the fishery and samples of "adult females" from our three areas (Fig. 3) was also rejected ($P < 0.001$). *Post hoc* tests (Table 3) showed no significant differences between fishery-caught eastern spinner dolphins and the photographic

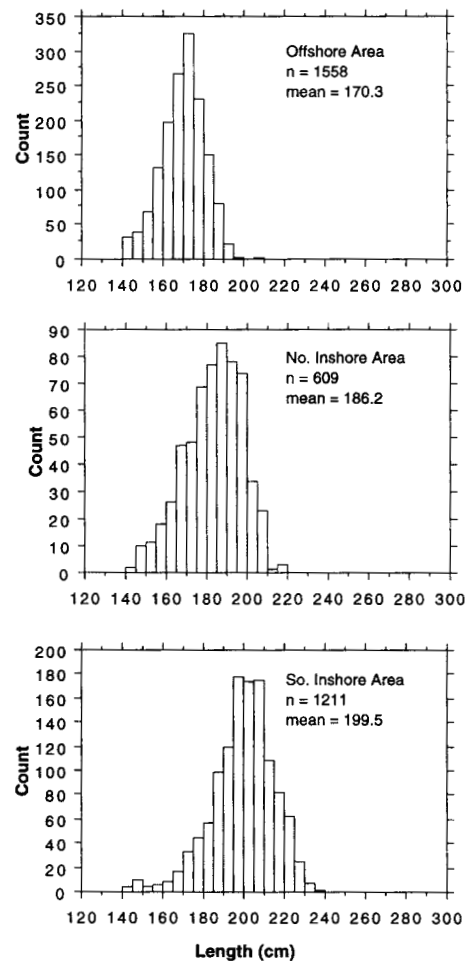


Figure 2. Histograms of lengths of spinner dolphins (both sexes, > 140 cm) from the offshore, northern inshore, and southern inshore areas. All lengths were measured from vertical aerial photographs.

Table 2. Results of *post hoc* test (Tukey-Kramer) for comparisons of truncated length samples of spinner dolphins photographed in the northern inshore, offshore, and southern inshore areas. All lengths are from aerial photographs and are in cm. Differences between means of regional length samples (Diff.) and critical differences (Crit. diff.) for 0.05 significance level are listed.

Comparison	Diff.	Crit. diff.	P
Offshore <i>vs.</i> N. inshore	15.86	1.50	<0.01
Offshore <i>vs.</i> S. inshore	29.14	1.20	<0.01
N. inshore <i>vs.</i> S. inshore	13.28	1.55	<0.01

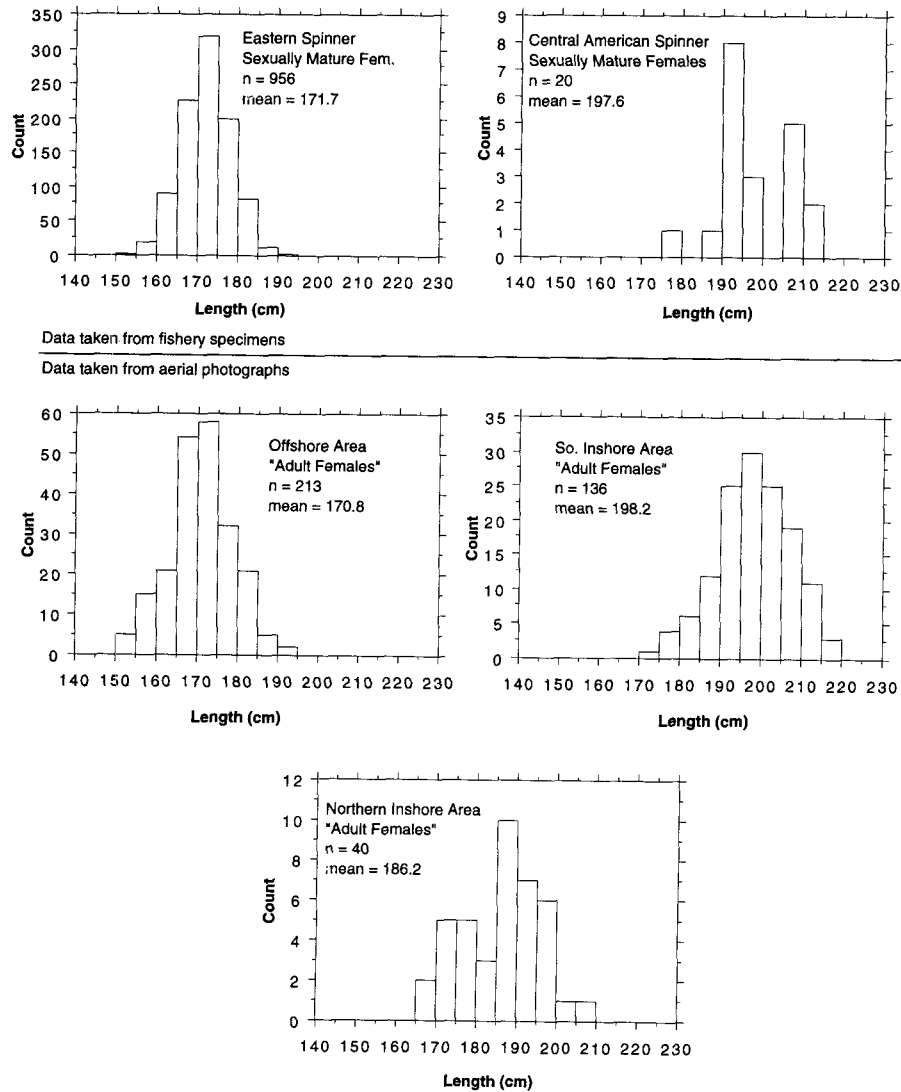


Figure 3. Histograms of lengths from fishery specimens of sexually mature female eastern and Central American spinner dolphins and photographed "adult female" spinner dolphins in the offshore, northern inshore, and southern inshore areas.

sample from the offshore area, and no difference between fishery-caught Central American spinner dolphins and the photographic sample from the southern inshore area. However, the photographic sample from the northern inshore area differed significantly from all other samples.

Because we found that the spinner dolphins from the northern inshore region were larger on average than those found offshore, we compared length samples of "adult females" from two schools photographed near the mouth of

Table 3. Results of *post hoc* tests (Tukey-Kramer) for comparisons between lengths from eastern and Central American spinner specimens (sexually mature females) and "adult females" photographed in the northern inshore, offshore, and southern inshore areas. All lengths are in cm. Differences between means of regional length samples (Diff.) and critical differences (Crit. diff.) for 0.05 significance levels are listed.

Comparison	Diff.	Crit. diff.	P
Offshore <i>vs.</i> Eastern	0.89	1.44	>0.05
Offshore <i>vs.</i> N. inshore	15.40	3.26	<0.01
Offshore <i>vs.</i> Central Amer.	26.81	4.43	<0.01
Offshore <i>vs.</i> S. inshore	27.40	2.08	<0.01
Eastern <i>vs.</i> N. inshore	14.51	3.06	<0.01
Eastern <i>vs.</i> Central Amer.	25.92	4.28	<0.01
Eastern <i>vs.</i> S. inshore	26.48	1.74	<0.01
N. inshore <i>vs.</i> Central Amer.	11.40	5.19	<0.01
N. inshore <i>vs.</i> S. inshore	11.97	3.41	<0.01
S. inshore <i>vs.</i> Central Amer.	0.56	4.54	>0.05

the Gulf of California (see Fig. 1) with lengths of "adult females" from the offshore and northern inshore regions. Our goal here was to test for evidence of mixing or a clinal change in average length at the boundary between the inshore and offshore strata. We found that the "adult females" photographed near the mouth of the Gulf of California, at the northern edge of the offshore sample, were not significantly different in length from the remainder of the eastern spinner sample, and that these "adult females" differed significantly from the northern inshore sample (Table 4).

DISCUSSION

In the areas sampled both photographically and by the purse-seine fishery, the same picture of spinner dolphin intraspecific stock structure emerges. Both sampling methods found the eastern spinner to be widely distributed offshore, while the larger Central American spinner is restricted to the continental shelf south of the Gulf of Tehuantepec. For these two subspecies of spinners, we found no significant difference in the means of length samples for adult female dolphins collected by the two methods.

Table 4. Results of *post hoc* tests (Tukey-Kramer) for comparisons between lengths of "adult females" from the northern inshore area, two schools from the offshore area closest to the northern shelf (mouth of Gulf) and the remainder of the offshore area sample. All lengths are from aerial photographs and are in cm. Differences between means of regional lengths samples (Diff.) and critical differences (Crit. diff.) for the 0.05 significance level are listed.

Comparison	Diff.	Crit. diff.	P
Offshore <i>vs.</i> mouth of Gulf	0.06	4.33	>0.05
Offshore <i>vs.</i> N. inshore	15.41	3.34	<0.01
N. inshore <i>vs.</i> mouth of Gulf	15.35	5.10	<0.01

North of Cabo Corrientes, the spinner dolphins that we photographed were intermediate in length between the eastern and Central American spinner subspecies. We found no evidence of mixing between the northern inshore and the offshore strata. Although spinner dolphins from this region were not recognized as unique in reviews of spinner dolphin morphology (Perrin *et al.* 1991, Douglas *et al.* 1992), some morphological evidence exists that supports our findings (Douglas *et al.* 1992).

Douglas *et al.* (1992) examined geographic variation in cranial morphology of spinner dolphins from the ETP by comparing measurements from specimens taken within 5° latitude-longitude blocks. The block at the extreme northeast of their grid consisted of three specimens taken from the Tres Marias region (LACM 54034, LACM 54035, USNM 88976). They reported a highly significant ($P < 0.001$) correlation between water depth and two morphological characters (length of brain case and width of temporal fossa). This analysis separated blocks containing Central American spinner dolphins and spinner dolphins from the Tres Marias region (their block 0812) from the eastern and Hawaiian spinner dolphins from deeper waters. Throughout their analysis, the Tres Marias block was consistently grouped with blocks including Central American spinners for specific cranial characters (longer tooth rows, more teeth, narrower skulls at the parietals, narrower temporal fossa).

Our analyses and those of Douglas *et al.* (1992) indicate that the spinner dolphins found along the continental shelf north of Cabo Corrientes are morphologically modally different from other spinners in the ETP. We have provisionally designated this form the "Tres Marias spinner dolphin," after the small group of islands located along the southern edge of their habitat. We recommend that the Tres Marias form be recognized as a unique stock of spinner dolphins whose range is not yet well defined. Future morphologic and genetic studies may indicate that it should be recognized as a subspecies distinct from *S. l. orientalis*.

Other observations on the Tres Marias spinner dolphin—Tres Marias spinner dolphins are very similar to the eastern form in external morphology, and even very experienced observers would not likely be able to distinguish them from the eastern subspecies at sea. Like the eastern spinner dolphin, this form is long, slender, and uniform medium-to-dark gray. The dorsal fin is triangular to forward canted, and pronounced ventral keels are present on some individuals (Fig. 4).

The schooling behavior of the Tres Marias spinner dolphin is similar to that observed for Central American spinners (Scott and Perryman 1991). The schools are relatively large and more tightly packed than those typical of eastern spinner dolphins. The Tres Marias spinners avoided the research vessel in a lethargic manner, and several individuals from each school came to the ship and rode the bow wave. Several high leaps and spinning behaviors were noted. Two of the three schools that we photographed were associated with yellowfin tuna, and one school included a small number of pantropical spotted dolphins (about 1%–5% of the school). The few spotted dolphins sighted with this school may have been herded together with the spinners by the approach

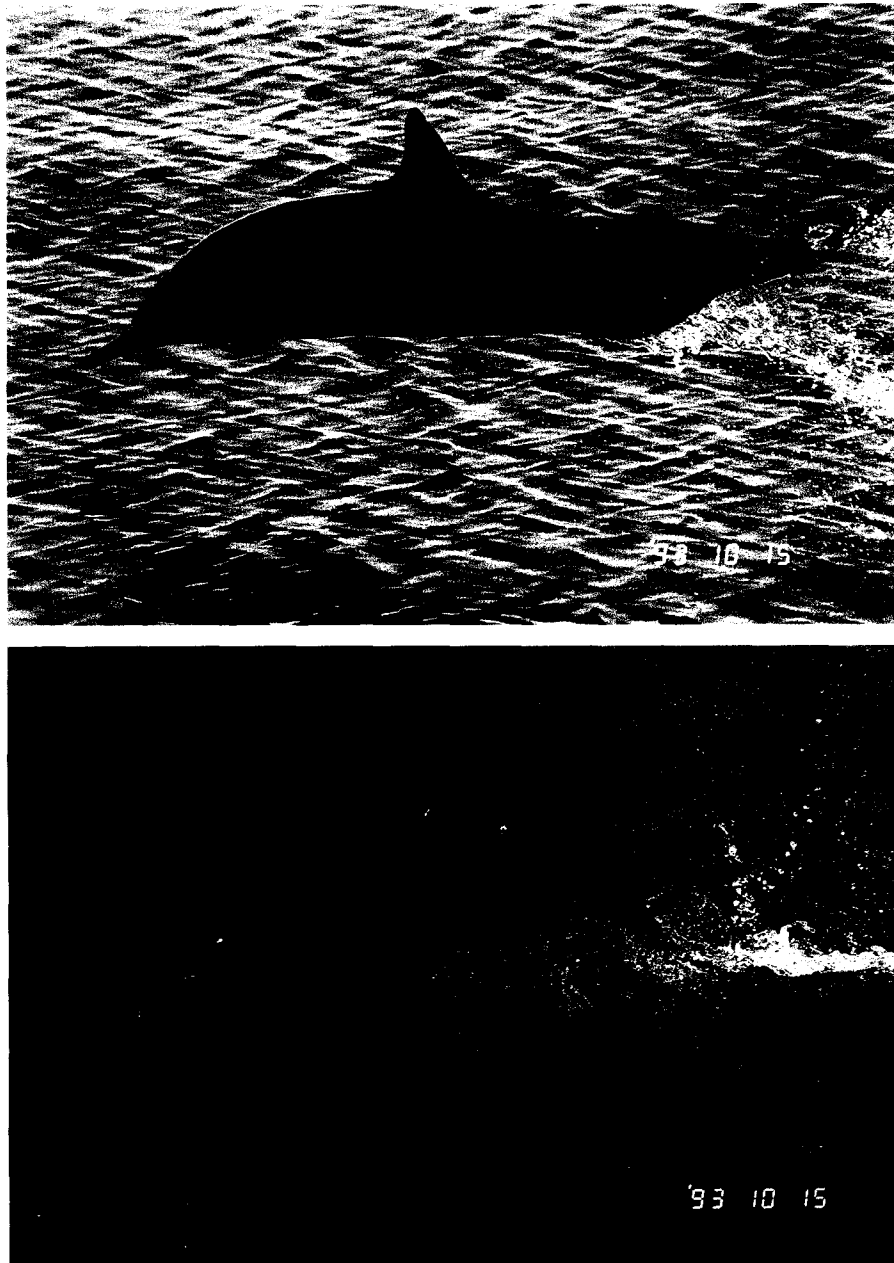


Figure 4. Photographs of dolphins identified as Tres Marias spinner dolphins based on lengths measured from aerial photographs (school #2 from Table 1). Note forward-canted dorsal fin and ventral keel on the dolphin in 4a and the triangular fin and long rostrum on the dolphin in 4b. Both photographs were taken by Scott Benson.

of our research vessel; this may not indicate that this form commonly associates with spotted dolphins.

Our data corroborated reports from fishery-derived data where significant samples were available, but we found that reliance on data only from the fishery resulted in an incomplete picture of spinner dolphin stock structure in the ETP. These results illustrate that one should make use of the broadest suite of data possible, including fishery-independent data, when making management decisions.

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